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Bedrock modulates the elevational patterns of soil microbial communities

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ABSTRACT

Elevational gradients are often used to reveal how soil microorganisms will respond to climate change. However, inconsistent microbial distribution patterns across different elevational transects have raised doubts about their practical applicability. We hypothesized that variations in bedrock, which influence soil physical and chemical properties, would explain these inconsistencies. We therefore investigated soil microbial communities (bacterial and fungal) along two adjacent elevational transects with different bedrocks (granite vs. slate) in a subtropical forest. Our findings reveal that soil microbial communities are shaped by complex interactions between bedrock type and environmental factors along elevational gradients. Bacterial biomass was higher on slate, whereas fungal biomass was higher on granite. On granite, both bacterial and fungal biomass increased with elevation, whereas divergent patterns were observed on slate, likely due to the distinct soil properties or combinations of properties influencing microbial biomass on each bedrock. Bedrock and elevation strongly influenced microbial beta-diversity, with beta-diversity on granite driven primarily by soil total phosphorus and moisture, and on slate by soil organic carbon and pH. In contrast, alpha-diversity was impacted less by bedrock and elevation, but its relationship with environmental factors varied markedly between bedrock types. Overall, our results highlight the critical influence of bedrock in determining soil microbial community structure along elevational gradients and their potential responses to climate change.

1. Introduction

As a proxy for the impacts of climate change on microbial communities, elevational gradients provide unique insights into the regulatory mechanisms governing the spatial distribution of soil microorganisms (Sundqvist et al., 2013). Studying the distributions of soil microorganisms along elevational gradients not only reveals the mechanisms structuring soil microbial communities (Nottingham et al., 2018; Peters et al., 2019), it also useful for understanding the impacts of climate

change on soil biogeochemical cycles (Bahram et al., 2018; Hartmann and Six, 2022; Philippot et al., 2023). Numerous studies of the elevational patterns of soil microbial communities have emerged over the past two decades (Bryant et al., 2008; Fierer et al., 2011; He et al., 2020; Hendershot et al., 2017). However, these studies have not found consistent trends in microbial biomass or community α -diversity: linear increases, linear decreases, unimodal and concave trends have all been detected (He et al., 2020; Hendershot et al., 2017; Wang et al., 2024). Environmental explanations for these disparate patterns include

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climatic regions (He et al., 2020), vegetation types (Li et al., 2016), or microclimate variation (Ma et al., 2022). However, the type of soil parent material –known as “bedrock”– may also explain complex elevational patterns.

Spatial variations in soil microbial communities are influenced strongly by soil properties (Fierer et al., 2009; Ni et al., 2022; Seaton et al., 2020). The factors shaping these communities are often determined by specific combinations of local soil characteristics. For example, soil pH is a well-established driver of bacterial community composition, particularly in acidic soils (Griffiths et al., 2011; Tripathi et al., 2018). Similarly, the availability of nutrients such as nitrogen and phosphorus plays a key role in regulating microbial dynamics, especially in nutrient-limited ecosystems (Delgado-Baquerizo et al., 2017). While climatic factors along elevational gradients tend to follow predictable trends within similar climate zones, the responses of soil microbial communities to climate change may vary depending on underlying soil conditions (e.g., acidic vs. neutral soils; nutrient-limited vs. nutrient-rich environments). Bedrock, as the parent material for soil formation, influences a wide range of soil physico-chemical properties, including pH, texture, and P levels (Augusto et al., 2017; He et al., 2021; Porder and Ramachandran, 2013; Spinola et al., 2022; Zeng et al., 2023). Consequently, soil microbial communities on different bedrock types may exhibit distinct responses to climate changes along elevational gradients, reflecting the unique soil environments created by bedrock characteristics. In the present study, we explored the extent to which bedrock can explain complex elevational patterns.

Bedrock varies in mountainous regions at both regional and local scales (Antonelli et al., 2018), affecting the spatial patterns of soil microorganisms (He et al., 2024; Hu et al., 2020; Li et al., 2018). However, only two studies have revealed that differences in bedrocks can affect the response of soil microbes to elevational gradients (Bhople et al., 2019; Singh et al., 2014). Singh et al. (2014) established two adjacent elevational transects on Mount Hana in South Korea, one on basalt and one on coarse-grained basalt. They observed a triple-curve in bacterial species richness on the basalt and a concave pattern on the coarse-grained basalt. Bhople et al. (2019) showed a linear increase in soil microbial biomass on basaltic bedrock and acidic soils, and a unimodal pattern on limestone bedrock with pH neutral soils.

Studies focusing on the influence of bedrock on elevational patterns of soil microbes are remarkably scarce, and these studies often concentrate on a single feature of soil microbial communities, such as biomass, or community α -diversity. Biomass, α -diversity, and β -diversity are crucial characteristics of soil microbial communities, usually regulated by different factors. Soil microbes are often carbon (C) limited, which is why microbial biomass is predominantly driven by the availability of labile C (He et al., 2020). α -diversity is more responsive to variations in soil pH (Fierer, 2017; Looby and Martin, 2020), particularly within acidic environments (Calderón-Sanou et al., 2022). The β -diversity of soil microbial communities, which describes the compositional variation among microbial communities across different environments, is influenced by a complex interplay of factors (Chen and Lewis, 2023). With such diverse characteristics of microbial communities being regulated by an assortment of environmental factors, it is no surprise that the interactions between bedrock, elevation, and soil microbial communities are extremely intricate.

In accordance with our hypothesis that bedrock modulates the environmental factors regulating soil microbial communities at different elevations, we anticipate significant differences in microbial community composition between the two bedrock types. Specifically, we expect to find that: (1) Soil microbial biomass, α -diversity, and β -diversity differ between bedrock types. We expect microbial biomass and α -diversity to increase on the slate transect due to its higher SOC, phosphorus levels, and pH (He et al., 2021). (2) Bedrock type will govern the relationship between elevation, microbial biomass and α -diversity. Given that key environmental conditions structuring microbial communities differ on different bedrocks, we also predict that (3) factors driving β -diversity

along the elevational gradient will vary between the two bedrocks, and similar environmental conditions may shape microbial community patterns differently on different bedrock types.

2. Materials and methods

2.1. Study sites

We worked in the Chebaling National Nature Reserve in the Guangdong Province of southern China (114°09′–114°16′E, 24°40′–24°46′N). The climate is a typical subtropical monsoon (He et al., 2021). The geological structure of the Reserve belongs to the South China fold system. Elevation ranges from 330 m above sea level to 1,256 m.a.s.l. Cambrian and Ordovician strata are present in the northwest section. Northeast-southwest slate was formed after fold-fracture. The middle and south are Cambrian strata, forming slate mountains. The northern parts experienced intrusion of Jurassic plutonic rocks, forming acid plutonic rock mountains. Soils are classified in the Ultisol order and the Udult suborder based on the USDA soil classification system (Zhou et al., 2013).

We identified two adjacent mountains with different bedrocks (granite and slate) in the Chebaling National Nature Reserve (He et al., 2021). The geographic distance between the two mountains does not exceed 10 km. The vegetation on both mountains is well-preserved subtropical evergreen broad-leaved forest. The forest on the granite bedrock is dominated by *Schima superba*, *Machilus chinensis*, and *Eurya nitida*, while the forest on the slate bedrock is dominated by *Machilus chinensis*, *Eurya nitida* and *Rhododendron simsii*. A total of 18 sites were established along two elevational transects (Fig. S1), with nine sites on each bedrock. Plots were distributed at about 100-m intervals in elevation (determined by GPS) within each transect, with elevations ranging from 410 to 1,080 m.a.s.l. on the granite bedrock and 350 to 1,120 m.a.s.l. on the slate bedrock. To reduce the influence of aspect, sampling plots were located on the south side of any microtopography at each site.

2.2. Sampling and analytical methods

All plots (40 m × 40 m) were sampled in October 2018. All trees with a diameter at breast height above 1 cm were recorded in each plot. We estimated the forest above-ground biomass (AGB) using diameter at breast height of each tree and allometric relationships (Réjou-Méchain et al., 2017). We installed a Micro Station Data Logger (USA, HOBO, H21-002) in each plot, with two probes inserted into the soil (at a depth of approximately 10 cm) which monitored soil temperature and moisture. Recordings were taken hourly from July 13, 2018, to July 13, 2019. Here, we use the data collected over the entire year to calculate the soil mean annual temperature (MAT) and moisture, which we use to explain the spatial variation of soil microbial community characteristics.

Volumetric soil samples were taken to determine soil bulk density. Soil depth was more than 100 cm in all but two of the high elevation sites in the slate transect. In these two plots, soil depth was roughly 60 cm. These shallow soil depths were likely due to severe erosion on the steeper slopes. Five subplots (10 × 10 m) were randomly selected at each site. We removed the leaf litter from the forest floor and collected topsoil to a depth of 20 cm using a stainless soil corer (inner diameter = 3.5 cm). We collected six random soil cores and homogenized them into composite samples for each subplot. A total of 90 soil samples (i.e. 18 plots × 5 subplots) were collected and transported on ice directly to the laboratory. Each soil sample was then passed through a 2-mm sieve before being divided into two subsamples: one was stored at –80 °C for phospholipid fatty acid (PLFA) analysis and high-throughput sequencing (HTS), and one was air-dried at room temperature for the measurement of soil physicochemical properties in the laboratory.

We measured soil pH with a PHS-3C pH acidometer (soil–water ratio of 1:5) and used dry combustion with an elemental analyser (Perkin

Elmer 2400 Series II) to measure soil organic carbon (SOC) and total N (TN) concentrations. Soil total P (TP) concentration was measured using a nitric acid–perchloric acid digestion, followed by a colorimetric analysis (Murphy and Riley, 1962) using a UV–Vis spectrophotometer (UV1800; Shimadzu, Kyoto, Japan). We measured particle size distribution using a laser particle analyzer based on the laser diffraction technique operating over a range of 0.02–2000 μm (Mastersizer 2000 particle size analyzer, Malvern Instruments, Ltd., UK).

We used a modified PLFA analysis (Frostegård and Bååth, 1996) to determine bacterial and fungal biomass. The abundance of individual fatty acids was expressed as μg per g of dry soil. Concentrations of each PLFA were calculated based on the 19:0 internal standard concentrations and microbial biomass was expressed as the sum of identifiable PLFAs. We chose a set of fatty acids to represent bacterial PLFAs. Bacterial PLFAs were obtained by summing the phospholipid fatty acid 14:00, 15:00, 16:00, 18:00, 13:0 anteiso, 13:0 iso, 14:0 iso, 14:1 ω 5c, 15:0 anteiso, 15:0 iso, 15:1 ω 6c, 16:0 iso, 16:1 ω 5c, 16:1 ω 7c, 17:0 anteiso, 17:0 cyclo ω 7c, 17:0 iso, 18:1 ω 7c, 18:1 ω 9c, 19:0 cyclo ω 7c, and 19:0 cyclo ω 9c contents. Gram-positive bacteria were identified by branched-chain fatty acids, including 13:0 anteiso, 13:0 iso, 14:0 iso, 15:0 anteiso, 15:0 iso, 16:0 iso, and 17:0 anteiso and iso. Gram-negative bacteria were distinguished by monounsaturated and cyclopropyl fatty acids, specifically 14:1 ω 5c, 15:1 ω 6c, 16:1 ω 5c, 16:1 ω 7c, 17:0 cyclo ω 7c, 18:1 ω 7c, 18:1 ω 9c, 19:0 cyclo ω 7c, and 19:0 cyclo ω 9c. The sum of 18:2 ω 6c and 18:3 ω 6c represented fungal PLFAs.

Soil DNA was extracted from composite soil samples using the FastDNA SPIN Kit for Soil (MP Biomedicals, Heidelberg, Germany) and purified by agarose gel electrophoresis. The quality of the DNA samples was checked on a spectrophotometer (NanoDrop, ND2000, Thermo-Scientific, USA). Total DNA was used for high-throughput sequencing on an Illumina MiSeq platform (San Diego, CA, USA). The bacterial V4 hypervariable region of the 16S rRNA gene and fungal internal transcribed spacer (ITS) region was amplified using the primer pair 505F/816R (5'-GTGCCAGCMGCCGCGG-3'/5'-GGACTACHVGGGTWTCTA AT-3') (Caporaso et al., 2011) and ITS1F/ITS2 (5'-GGAAGTAAAAGTCGTAACAAGG-3'/5'-GCTGCGTCTTCATCGATG-C-3') (Shen et al., 2020) along with the Illumina adaptor sequence and barcode sequences, respectively.

The raw sequence data were processed and analyzed using QIIME Pipeline (Caporaso et al., 2011). To improve sequence quality we removed average quality (value ≤ 20) sequencing reads with ambiguous nucleotides in barcodes, and homopolymer reads between 8 bp and 150 bp in length. Paired ends were joined with FLASH (Magoc and Salzberg, 2011). Chimeric sequences were detected and eliminated using the Uchime algorithm (Edgar, 2011). All sequences were clustered into operational taxonomic units (OTUs) at a 97 % identity threshold. Finally, the representative sequences of each OTU were classified against the RDP 16S rRNA database for bacteria and UNITE Fungal ITS database for fungi with an 80 % confidence threshold. The resultant OTU abundance tables from these analyses were rarefied to an even number of sequences per sample to ensure equal sampling depth (26,160 and 26,760 for 16S rDNA and ITS, respectively). To minimize the influence of potentially spurious OTUs, we excluded those with a total read count below 50 or present in fewer than five samples after rarefaction. All subsequent analyses of α - and β -diversity were conducted based on this filtered OTU table. The raw reads have been deposited into the National Centre for Biotechnology Information (NCBI) Sequence Read Archive database (PRJNA1177672).

2.3. Statistical analyses

We used Wilcoxon tests to assess differences in microclimate, plant traits, and soil properties between granite and slate bedrocks. To evaluate elevational trends, we applied univariate linear regression models, while multivariate linear regression models were used to examine soil microbial community responses across different elevations and bedrock

types, as well as to identify interactive effects. Model fit was evaluated using Akaike's Information Criterion (AIC), with the model having the lowest AIC score selected as the best fit.

Spearman correlation analyses were conducted to determine whether bedrock type influenced relationships between environmental variables and soil microbial communities. Additionally, we applied multiple regression models to investigate associations between microbial variables (bacterial and fungal biomass, biomass ratios, and alpha diversity indices) and a range of environmental predictors, including soil properties, i.e., pH, moisture, clay content, soil organic C (SOC), soil P, soil C-to-N ratio (C:N), soil C-to-P ratio (C:P), soil N-to-P ratio (N:P), plant traits (above-ground biomass and plant Shannon diversity), and climatic factors (mean annual temperature). Multicollinearity among predictors was assessed using Variance Inflation Factor (VIF) values calculated with the *vif* function from the *car* package. Initial VIF analysis revealed high collinearity among certain soil nutrient ratios (soil C:P and soil N:P), with VIF values exceeding 100; thus, these variables were excluded, reducing the VIF of all remaining predictors to below 5. To examine interactions between environmental predictors and bedrock type, we incorporated selected interaction terms (bedrock:TP, bedrock:moisture, bedrock:pH, and bedrock:MAT) aligned with our research questions. Due to the limited sample size, we focused on these specific interactions rather than including all possible terms. Stepwise model selection using AIC was performed with the *dredge* function from the *MuMIn* package to identify best-fit models for each microbial variable, allowing for retention of the most informative predictors while optimizing model performance.

We calculated the Chao1 index, Shannon, and Inverse Simpson diversity index as α -diversity indices of soil microbial communities. Shannon index is defined as $H = -\sum_i^i P_i \log P_i$, where P_i is the proportional abundance of species i . Inverse Simpson index is defined as $1/D$, where $D = \sum P_i^2$. We used the Bray-Curtis-dissimilarities-based principal components analysis (PCoA) to assess differences (β -diversity) in microbial communities in different sites and bedrocks. We performed square root transformations of the OTU relative abundances before the PCoA. We performed distance-based Redundancy Analysis (db-RDA) of the correlation between predictor variables and microbial composition. We calculated these diversity indices and conducted these ordination analyses using the *vegan* R package (Oksanen et al., 2020). We performed a Principal Component Analysis (PCA) to visualize the variation in environmental variables across elevational gradients on two bedrock types. The analysis was conducted using the *PCA* function from the *FactoMineR* package. A biplot was created using *fviz_pca_biplot* from the *factoextra* package. We used a neutral community model (NCM) (Sloan et al., 2006) to test whether deterministic or stochastic processes were structuring the microbial communities. We used *Hmisc*, *minpack.lm* and *stats4* packages for the NCM, with default parameters for model fitting.

All statistical analyses were performed using R (R Core Team, 2023) and graphs were generated with the *ggplot2* package (Wickham, 2016).

3. Results

3.1. Effects of elevation and bedrock on soil characteristics

Wilcoxon tests showed no significant differences in soil MAT, moisture, and SOC concentration between the granite and slate transects (Table S1). AGB, soil C:N, C:P, N:P ratios, and soil silt and sand contents were higher on the granite transect, whereas plant diversity, soil pH, bulk density, TN, TP, and clay content were lower on the granite than on the slate transect. Univariate linear regression models revealed a consistent pattern of significant declines in MAT, plant diversity and soil pH with elevation, and an increase in SOC, TN, TP and silt content across both bedrock types (Figs. S2 and S3). Soil clay content and moisture showed no significant elevational trend along either transect (Fig. S3). AGB decreased with elevation on the granite but showed no significant

trend on the slate (Fig. S2). PCA results revealed a clear separation of sampling sites along PC1 (Fig. S4). Key variables associated with PC1, such as soil P, C:N, C:P, N:P, clay, and moisture, appear to be major environmental drivers of microbial community differences between the two bedrocks. Variables closely aligned with PC2, including elevation, MAT, SOC, and pH, are likely primary drivers of microbial community changes along the elevational gradient within each transect.

3.2. Effects of elevation and bedrock on soil microbial biomass

Bacterial biomass was slightly higher on slate, whereas fungal biomass was higher on granite (Table 1). Consequently, the bacteria-to-fungi biomass ratio (B/F) was significantly higher on slate than on granite. Given that Gram-positive bacteria are ecologically and functionally more similar to fungi, our findings align with this pattern: the Gram-positive to Gram-negative bacteria ratio (G+/G- ratio) was significantly higher on granite than on slate. Notably, both bacterial (B) and fungal (F) biomass, along with the G+/G- ratio increased significantly with elevation on the granite but not on the slate transect; B/F ratios showed no significant linear trends on either bedrock (Fig. 1). Multivariate linear regression models confirmed significant impacts of elevation and bedrock on microbial biomass characteristics, including significant interactive effects for bacterial and fungal biomass but not for B/F ratios or G+/G- ratios (Table 2).

The best models selected through stepwise regression provided strong explanatory power for variations in microbial biomass, with adjusted R^2 values ranging from 0.45 to 0.71 (Table 3). Soil microbial biomass was shaped significantly by multiple environmental factors and their interactions with bedrock type. For bacterial biomass, SOC, TP, and the soil C:N ratio were key factors, with positive associations observed for soil C and P, and a negative association with the C:N ratio. Fungal biomass was also influenced by SOC, C:N ratio, and TP, though the impacts of moisture and MAT varied depending on bedrock type. The B/F biomass ratio was shaped by soil moisture, plant Shannon diversity, and TP, with an interaction between moisture and bedrock type. Additionally, the G+/G- ratio was driven by soil clay content, MAT, and pH, with a significant interaction between TP and bedrock type.

Spearman correlations corroborated the multiple regression results (Tables S2 and S3). On the granite transect, bacterial biomass was strongly associated with SOC and TP, whereas on slate, no significant correlations were observed. Fungal biomass on granite correlated positively with SOC and the soil N:P ratio, while being negatively associated with AGB and MAT. On slate, fungal biomass correlated only with moisture. The B/F ratios on granite were positively linked with soil TP and negatively to moisture, whereas on slate, they correlated negatively with moisture. Additionally, the G+/G- ratios showed a strong positive correlation with the soil N:P ratio on granite and a negative correlation with MAT on slate.

Table 1

Results of the Wilcoxon test to compare the mean values of soil microbial biomass and α -diversities between two bedrock transects. Significantly higher mean values are in bold. Unit of biomass is $\mu\text{g g}^{-1}$ soil.

Variable	Granite (Mean \pm SD)	Slate (Mean \pm SD)	w	p
Fungal biomass	1.33 \pm 0.54	1.09 \pm 0.37	1267	0.040
Bacterial biomass	38.62 \pm 14.2	42.95 \pm 9.58	791	0.074
Bacteria to fungi ratio	30.79 \pm 10.49	42.28 \pm 11.66	476	<0.001
Gram + to Gram- ratio	0.81 \pm 0.08	0.72 \pm 0.05	1634	<0.001
Bacterial Chao1	3036 \pm 294	3344 \pm 349	520	<0.001
Bacterial Shannon	5.89 \pm 0.2	5.95 \pm 0.27	864	0.234
Bacterial inv-Simpson	104 \pm 29	82 \pm 28	1413	0.001
Fungal Chao1	1237 \pm 187	1364 \pm 209	695	0.010
Fungal Shannon	4.12 \pm 0.48	4.03 \pm 0.68	1060	0.706
Fungal inv-Simpson	18 \pm 8	16 \pm 9	1119	0.394

3.3. Effects of elevation and bedrock on soil microbial community diversity and composition

Microbial richness, as indicated by Chao1 indices, was consistently and significantly higher on slate for both bacterial and fungal communities (Table 1). In contrast, Shannon indices showed no significant differences between bedrock types for either bacterial or fungal communities, indicating comparable overall diversity. The inverse Simpson index, however, was significantly lower for bacterial communities on slate than on granite, suggesting reduced evenness and potential dominance by a few species on slate. Interestingly, soil microbial α -diversity, encompassing Shannon and inverse Simpson indices, showed no clear elevational trends (Fig. 2). Multivariate linear regression analyses confirmed these observations, identifying significant differences between bedrock transects in the Chao1 and inverse Simpson indices for bacteria, and in the Chao1 index for fungi, but not in other α -diversity measures. Additionally, elevation significantly influenced only the fungal Chao1 index, with no observable effect on other α -diversity indices or significant interactions between elevation and α -diversity (Table 2).

Regression models for diversity indices showed lower explanatory power compared with biomass (adjusted $R^2 = 0.20$ – 0.38 ; Table 4). Bacterial Shannon index was significantly affected by clay content, MAT, moisture, and pH, while the bacterial inverse Simpson index was associated with soil C, P, and a moisture-bedrock interaction. Both the fungal Shannon and inverse Simpson indices were influenced by soil P, soil C, and pH, with strong effects from interactions between these variables and bedrock type; soil P, in particular, played a prominent role in shaping fungal community diversity.

Spearman correlation analysis indicated that the Shannon index of the bacterial community correlated positively with soil pH on both granite and slate transects (Tables S2 and S3). The inverse Simpson index of bacteria correlated positively with soil C:P and N:P ratios on granite but showed no significant relationship on slate. The fungal community's Shannon index correlated negatively with MAT on both bedrocks, and additionally with clay content on granite. On slate, it correlated significantly with TP, C:P, and N:P. The inverse Simpson index for fungi correlated negatively with clay on granite, whereas on slate it showed significant correlations with soil pH, C:N, C:P, N:P, and other environmental factors (Table S3).

Principal Components Analysis results highlighted clear differences in beta-diversity, i.e., the composition of soil microbial communities (bacterial and fungal), across different bedrock types (Fig. 3a and b). Results of db-RDA revealed that the compositions of soil bacterial and fungal communities were determined primarily by the soil C:P and N:P ratios and TP content (Fig. 3a). These findings indicate that variations in phosphorus level were key in driving the differences in community composition observed between the bedrocks. Further db-RDA on individual bedrock types revealed that on granite, soil TP content and moisture were crucial in shaping both bacterial and fungal communities (Fig. 3c and e). Conversely, on slate, SOC and soil pH were the dominant factors influencing bacterial communities (Fig. 3d), whereas moisture and clay content significantly affected fungal communities (Fig. 3f). This analysis suggests a role for bedrock in mediating species turnover along elevational gradients, with changes in soil P concentration and moisture levels being pivotal.

The fit of bacterial communities on granite to the NCM was higher ($R^2 = 0.92$; $N_m = 18943$) compared with slate ($R^2 = 0.90$; $N_m = 16458$) (Fig. S6a and b), suggesting the importance of stochastic processes in the assembly of these bacterial communities. In the case of the fungal communities, the fit to the NCM was comparable between granite ($R^2 = 0.62$; $N_m = 1237$) and slate ($R^2 = 0.62$; $N_m = 1209$), indicating no discernible difference in community assembly processes (Fig. S6c and d).

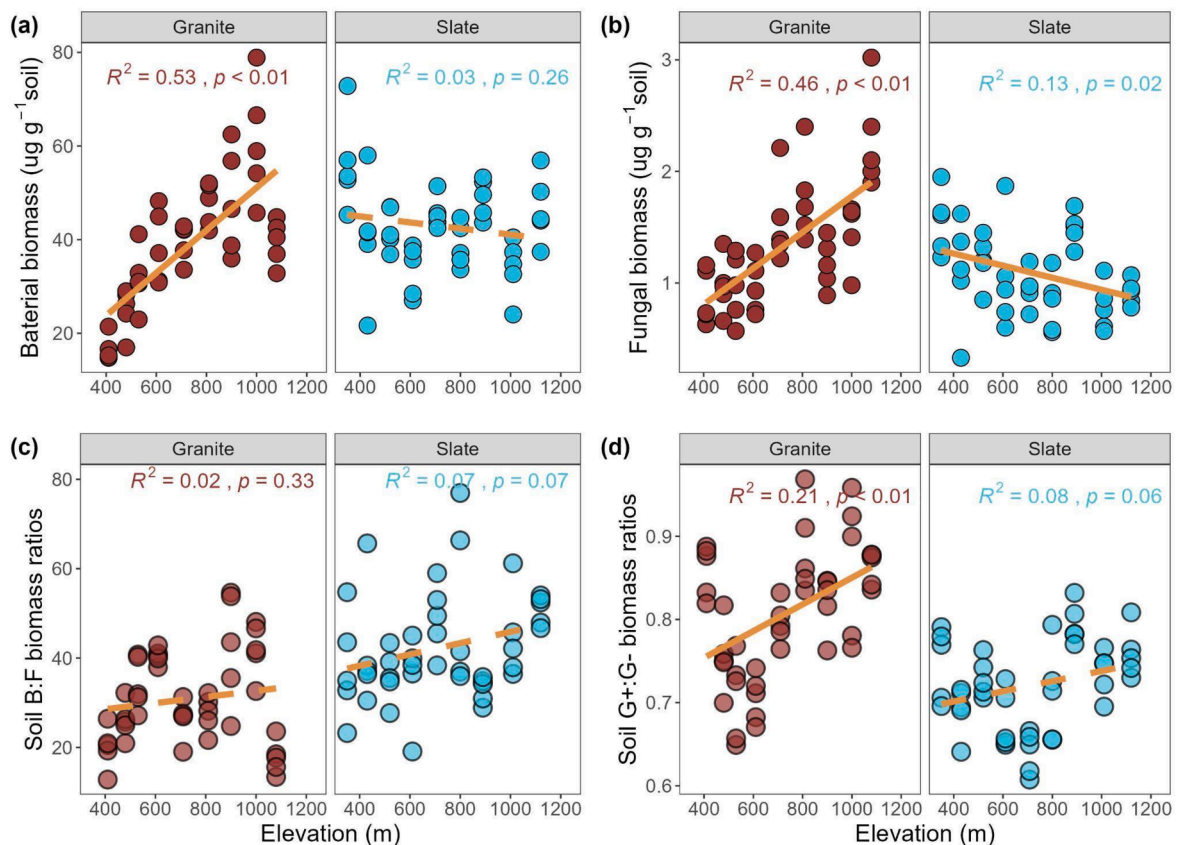


Fig. 1. Soil microbial biomass along elevational transects on granite and slate bedrock. (a) Soil bacterial biomass; (b) soil fungal biomass; (c) bacterial biomass to fungal biomass ratios; (d) gram-positive to gram-negative bacterial biomass ratios. Solid and dashed lines indicate significant ($p < 0.05$) and nonsignificant ($p > 0.05$) linear regression relationships, respectively.

Table 2

Effects of elevation and bedrock, and their interaction on the variations of soil microbial communities' characters. Numbers in the table are the standardized linear regression coefficients.

	Elevation	Bedrock	Elevation \times Bedrock	Adjusted R^2
Bacterial biomass	0.88***	0.36*	-1.01***	0.372
Fungal biomass	0.80***	-0.49*	-1.08***	0.373
B:F biomass ratio	0.19*	0.93***		0.231
G ⁺ to G ⁻ biomass ratio	0.31***	-1.06***		0.384
Bacterial Chao1 index	0.11	0.87***		0.182
Bacterial Shannon index	0.04	0.26		0.001
Bacterial inverse Simpson	0.17	-0.71***		0.140
Fungal Chao1 index	0.28**	0.62**		0.151
Fungal Shannon index	0.09	-0.12		0.001
Fungal inverse Simpson	-0.15	-0.20		0.001

Stars next to the numbers indicate significance in the regression model: *, **, *** indicates significance at the 95 %, 99 % and 99.9 % level, respectively; no star means $p > 0.05$.

4. Discussion

This study reinforces findings by [Bhople et al. \(2019\)](#) and [Singh et al. \(2014\)](#), confirming that bedrock composition plays a critical role in shaping soil microbial community responses along elevational gradients in subtropical mountain ecosystems. While this and previous studies

each focused on a single transect per bedrock type, together they provide robust evidence that bedrock type significantly influences microbial elevational patterns. Unique combinations and ranges of soil properties are established by different bedrock types, resulting in distinct microbial community distributions along elevation gradients. Moreover, the impact of specific environmental factors on microbial communities varies with bedrock type, highlighting the interactive effects between bedrock and environmental conditions on microbial distribution. These interactions deepen our understanding of the intricate dynamics of microbial communities and underscore the necessity to consider bedrock type when evaluating microbial responses to environmental changes.

4.1. Bedrock modulates the elevational patterns of soil microbial biomass

Bacterial and fungal biomass differed significantly on the contrasting bedrocks. Both transects were under similar climates, and we therefore conclude that differences in microbial biomass were likely caused by the variation of bedrock, which concurs with previous studies ([Deng et al., 2015](#); [Sun et al., 2016](#)). [Deng et al. \(2015\)](#), who worked in a similar subtropical monsoon climate, concluded that bedrock explained more variation in soil microbial biomass than land use, after discovering that microbial biomass in soil derived from granite was significantly higher than in soil derived from quaternary red earth and tertiary red sandstone. [Sun et al. \(2016\)](#) showed that agricultural soils derived from granite supported more microbial biomass than quaternary red clay soil and purple sandy shale, even after 40 years of agricultural use. These results further emphasize the fact that bedrock drives the spatial variation of soil microbial biomass.

Bacteria and fungi responded differently to the different bedrocks in our study, which is further evidence of the regulatory effects of bedrock on microbial communities. Bacterial biomass, particularly the amount of

Table 3

Summary of optimal model parameters for microbial biomass variables. This table presents the best-fit model results for microbial biomass variables, derived from an initial full model that included mean annual temperature (MAT), soil organic carbon (C), phosphorus (P), moisture, clay content, pH, carbon-to-nitrogen ratio (C:N), above-ground biomass (AGB), and plant Shannon diversity (Plant H). Additionally, interactions between bedrock type and specific environmental variables (soil P, moisture, pH, and MAT) were incorporated.

Microbial Variable	Predictors	Estimate	p-value	Adjusted R ²
Bacterial Biomass	Soil C	9.316	<0.001	0.625
	Soil C:N	-4.936	<0.001	
	Soil P	6.011	0.008	
	Clay	-2.065	0.070	
	MAT × Bedrock	4.294	0.022	
	Soil P × Bedrock	-11.818	<0.001	
Fungal Biomass	Soil C	0.267	<0.001	0.453
	Soil C:N	-0.216	<0.001	
	Soil P	-0.351	<0.001	
	Moisture × Bedrock	0.288	0.009	
	MAT × Bedrock	0.221	0.047	
Bacterial-to-Fungal Biomass ratio	Moisture	3.715	0.002	0.502
	Plant H	3.163	0.001	
	Soil P	6.042	<0.001	
	Moisture × Bedrock	-9.585	<0.001	
Gram ⁺ to Gram ⁻ bacteria biomass ratio	Clay	-0.015	0.046	0.710
	MAT	0.014	0.018	
	pH	-0.027	0.028	
	Soil P × Bedrock	0.060	0.020	

Gram-positive versus Gram-negative bacteria, was higher on slate than on granite. This can be attributed to slate's higher soil TN and TP contents, closer-to-neutral soil pH, and higher soil clay content, all of which favor bacterial growth. Bacteria, especially Gram-positive types, rely heavily on nutrient availability (Yu et al., 2022), are more sensitive to pH changes (Luan et al., 2023; Rousk et al., 2010), and benefit from the simplified physical conditions of soils richer in clay (Philippot et al., 2023). In contrast, fungi are better at extracting nutrients from decomposing organic matter (Koranda et al., 2014), and have a greater tolerance to pH changes (Rousk et al., 2010). Moreover, their multicellular, filamentous structure enables fungi to adapt to a variety of soil physical environments (Philippot et al., 2023). Furthermore, considering the competitive dynamics between fungi and bacteria (Bahram et al., 2018), the diminished bacterial biomass on granite reduces competition, potentially boosting fungal biomass. These mechanisms clarify why fungal biomass was higher on granite than on slate, providing insight into how bedrock variability distinctly influences bacterial and fungal communities.

As well as observing the effects of the bedrock itself on soil microbial communities, we also noticed inconsistencies in the elevational patterns of the soil microbial biomass along the two transects. On the granite, soil bacterial and fungal biomass increased with elevation, whereas on the slate, bacterial biomass showed no trend, and fungal biomass decreased slightly. Soil microbes usually need to derive energy and nutrients from soil organic matter, and as a result, their biomass is generally coupled with SOC concentration (He et al., 2020; Smith et al., 2021). However, in this study, such a relationship was observed only on granite; on slate, which had higher N and P levels, the biomass of bacteria and fungi did not show significant correlations with SOC, soil TP content, MAT, or other factors. This may be attributed to the fact that in nutrient-

abundant environments, especially with sufficient P, soil microbes experience lower nutrient limitations; and their reliance on the pathway of nutrient acquisition through the decomposition of organic matter might be comparatively weaker (Lang et al., 2016). This would certainly explain why microbial biomass was not correlated with SOC and TP concentrations on slate. These findings suggest that the bedrock, by influencing the P levels in the soil and indeed throughout the entire ecosystem, can impact the responses of soil microbial biomass to elevational gradients.

4.2. Bedrock modulates the elevational patterns of soil microbial community diversity

The higher Chao1 index for both bacterial and fungal communities on slate than on granite indicates greater microbial species richness in soils with higher nutrient content and pH (Xiao et al., 2022). However, neither the Shannon nor the inverse Simpson index on slate were significantly higher than on granite, suggesting that the increased richness on slate likely reflects a greater presence of rare or low-abundance taxa, reducing overall community evenness. In particular, the inverse Simpson index for bacterial communities was significantly higher on granite than on slate. This may be attributed to the lower P, moisture, and pH levels on granite, which may promote a broader range of microbial taxa that coexist more evenly. Conversely, the higher P, moisture, and pH levels on slate could favor a few dominant species, resulting in lower evenness despite the elevated species richness. Interestingly, unlike microbial biomass, neither bacterial nor fungal α -diversity varied significantly with elevation on either bedrock type, suggesting that soil microbial biomass and community α -diversity are regulated by different factors (Li et al., 2020; Ren et al., 2018). These distinct responses between microbial biomass and α -diversity, with their implications for ecosystem functioning, warrant further exploration.

With regard to those factors influencing α -diversity, our multiple linear models explained significantly less of the variation in α -diversity than in microbial biomass along the elevational gradient. Alongside the high explanatory power of neutral community models (NCM) on both bedrocks—especially with over 90 % for bacterial communities—our findings suggest that microbial community assembly along the elevation gradient was driven largely by stochastic processes, with environmental factors playing a lesser role. While we found significant relationships between soil pH and the Shannon indices for both bacteria and fungi, supporting the notion that microbial α -diversity is sensitive to soil acidity (Luan et al., 2023; Smith et al., 2021), α -diversity itself did not vary significantly with elevation. This is likely due to the relatively small pH fluctuations across the transects. Despite the limited explanatory power of our models, we observed that certain factors, such as soil phosphorus and moisture, had bedrock-specific effects on microbial α -diversity. These significant interactions indicate that although α -diversity did not shift noticeably with elevation, its relationship with environmental factors was still modulated by bedrock.

Our findings suggest that bedrock impacts the β -diversity of soil microbial communities. Bacteria and fungi displayed markedly distinct compositions across the two bedrocks. Our observation that bedrock influences the composition of soil microbial communities aligns with the conclusions of previous studies (Sheng et al., 2023; Tytgat et al., 2016; Weemstra et al., 2020; Xiao et al., 2022). Studies of different bedrocks have proposed different mechanisms for structuring soil microbial communities. For example, Tytgat et al. (2016) found that SOC content structured bacterial communities, whereas Sheng et al. (2023) concluded that soil pH structured the bacterial community composition among different bedrocks. We identified differences in soil P as the primary mechanism structuring soil microbial communities on the granite and slate bedrocks. On granite, soil TP content and moisture govern species turnover of both bacteria and fungi, which is supported by another study in nearby subtropical forest (Chen and Lewis, 2023). On slate, however, the influence of soil P on species turnover appeared

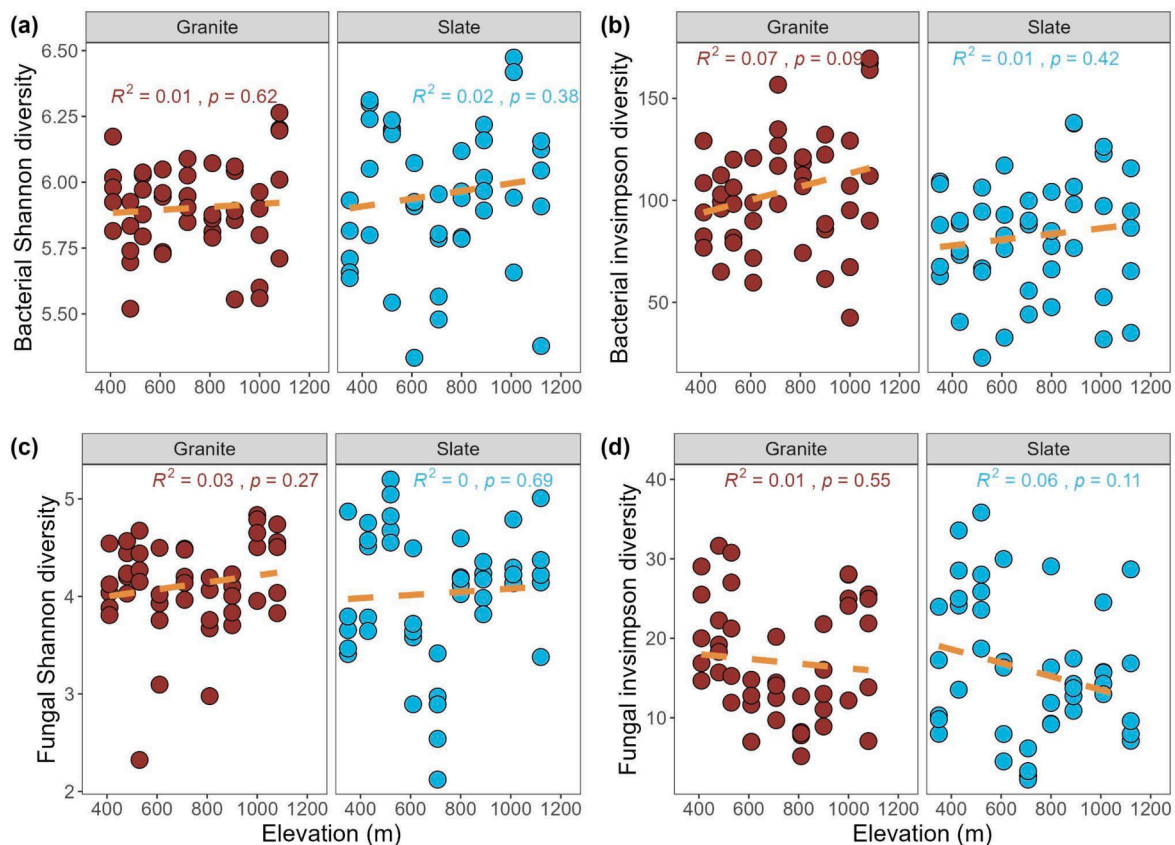


Fig. 2. Elevational patterns of soil microbial community α -diversities. (a and b) Shannon and inverse Simpson diversity index of bacterial communities, respectively; (c and d) Shannon and inverse Simpson diversity index of fungal communities, respectively. Dashed lines indicate nonsignificant ($p > 0.05$) linear regression relationships.

Table 4

Summary of optimal model parameters for microbial community diversity index. This table presents the best-fit model results for microbial diversity index, derived from an initial full model that included mean annual temperature (MAT), soil organic carbon (C), phosphorus (P), moisture, clay content, pH, carbon-to-nitrogen ratio, above-ground biomass (AGB), and plant Shannon diversity. Additionally, interactions between bedrock type and specific environmental variables (soil P, moisture, pH, and MAT) were incorporated.

Microbial Variable	Predictors	Estimate	<i>p</i> -value	Adjusted R ²
Bacterial Shannon index	Clay	0.068	0.008	0.271
	MAT	-0.098	<0.001	
	Moisture	-0.063	0.033	
	pH	0.075	0.004	
Bacterial inverse Simpson index	Soil C	9.249	0.013	0.202
	Soil P	-12.539	<0.001	
	Moisture \times Bedrock	15.275	0.020	
	Bedrock			
Fungal Shannon index	Soil P	-0.608	0.000	0.383
	AGB	-0.155	0.019	
	Moisture \times Bedrock	0.081	0.119	
	Bedrock			
	Soil P \times Bedrock	1.145	<0.001	
Fungal inverse Simpson index	Moisture	4.086	<0.001	0.332
	Soil P	-6.853	0.001	
	Soil C	-3.039	0.045	
	pH \times Bedrock	7.561	0.004	
	Soil P \times Bedrock	16.332	<0.001	
	Bedrock			

to be minimal. This could be due to P not being a limiting factor, as slate and its associated soils have high P concentrations. Together, these results indicate that bedrock type not only influences the composition of soil microbial communities, but also modulates the primary drivers of microbial community structure along elevational gradients.

Our results should be interpreted in light of the fact that our study was based on one elevational transect per bedrock type. Nonetheless, given the inconsistency of previous studies of soil microbial elevational patterns, including those based on single transects (e.g., Bayranvand et al., 2021; Peters et al., 2016; Zakavi et al., 2022), our findings provide relevant and valuable insights into how bedrock influences microbial community patterns along elevation gradients. Ideally, future studies should integrate multiple transects replicated within bedrock types to more thoroughly understand the responses of soil microbial communities to climate gradients.

5. Conclusion

We have shown that bedrock significantly influences soil microbial biomass and β -diversity, while having limited effects on α -diversity. Moreover, bedrock modulated the impacts of the elevation gradient on soil microbial biomass and β -diversity. This was likely an indirect process via the alteration of soil P content, C:P, N:P ratios, soil moisture, and pH. We believe that bedrock may explain some of the inconsistencies surrounding previous studies of the elevational patterns of soil microbial communities. We also anticipate that bedrock will modulate the impacts of climate change on soil microbial communities.

CRedit authorship contribution statement

Xianjin He: Conceptualization, Data curation, Investigation,

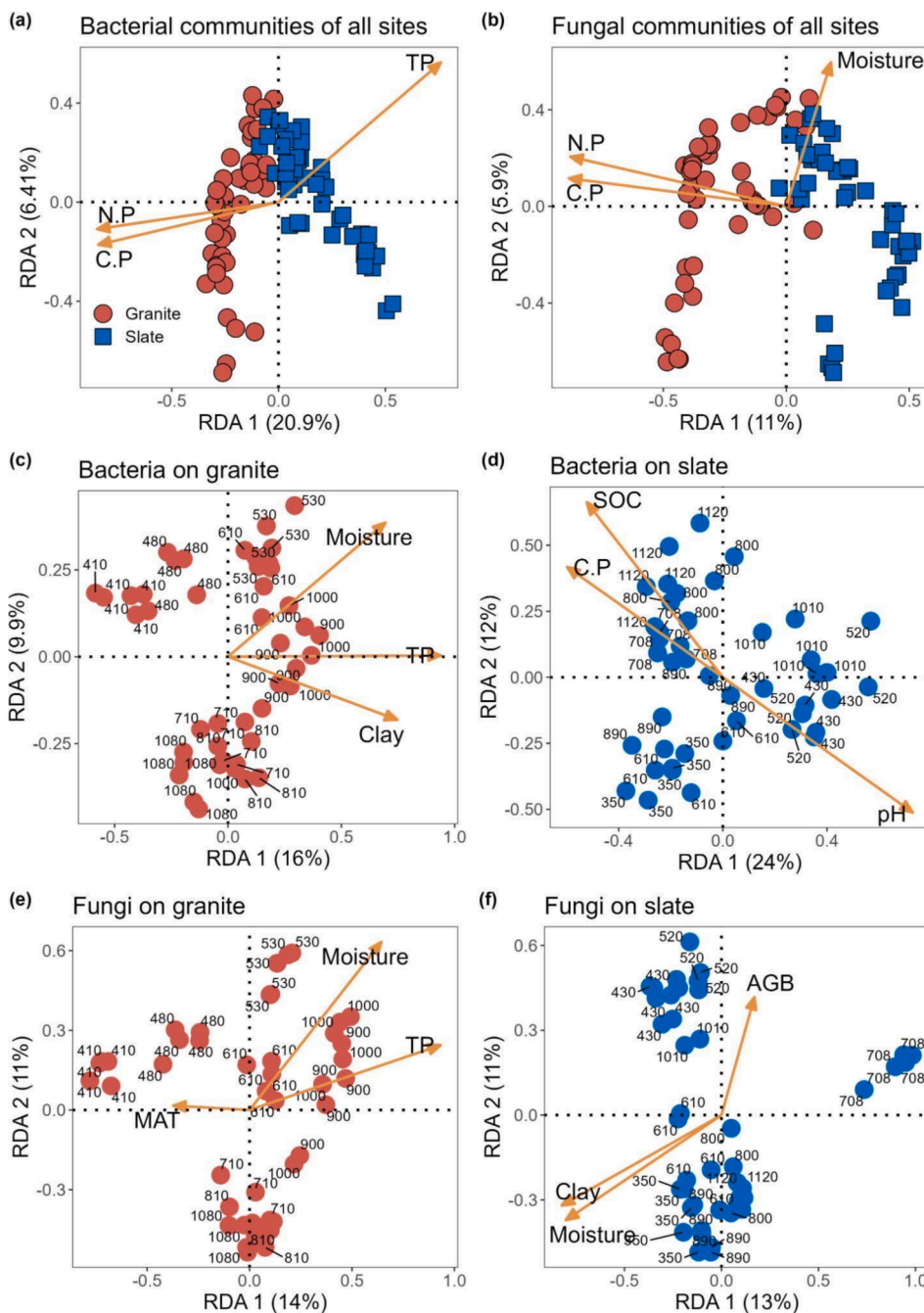


Fig. 3. Distance-based redundancy analysis (db-RDA) of the relationship between predictor variables and the Bray–Curtis dissimilarity distance between microbial communities. Dots indicate individual samples; the arrow lengths and directions correspond to the variance explained by the individual variables. The figure shows the three most important variables to keep it concise. Fig. S5 shows all the results for the variables' R^2 .

Visualization, Writing – original draft, Writing – review & editing. **Ruiqi Wang:** Data curation, Methodology, Writing – original draft, Writing – review & editing. **Daniel S. Goll:** Conceptualization, Writing – original draft, Writing – review & editing. **Laurent Augusto:** Conceptualization, Writing – original draft, Writing – review & editing. **Naiose Nunan:** Writing – original draft, Writing – review & editing. **M.D. Farnon Ell-gao:** Writing – original draft, Writing – review & editing. **Quanzhou Gao:** Data curation, Methodology. **Junlong Huang:** Formal analysis, Methodology, Writing – original draft, Writing – review & editing. **Shenhua Qian:** Formal analysis, Writing – original draft. **Yonghua Zhang:** Data curation, Methodology. **Zufei Shu:** Data curation. **Buhang Li:** Data curation, Methodology. **Chengjin Chu:** Writing – review & editing, Writing – original draft, Supervision, Funding acquisition,

Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.geoderma.2024.117136>.

Data availability

Data will be made available on request.

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